FOUNDATIONS
OF BEHAVIORAL NEUROSCIENCE

NEIL R. CARLSON

NINTH EDITION

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FOUNDATIONS OF BEHAVIORAL NEUROSCIENCE

NINTH EDITION

Neil R. Carlson
University of Massachusetts, Amherst

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Text Font: *10/12 Minion Pro*

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Library of Congress Cataloging-in-Publication Data

Carlson, Neil R.
Foundations of behavioral neuroscience / Neil Carlson.—9th ed.
p. cm.
Includes bibliographical references.
I. Title. 1. Nervous System Physiological Phenomena. 2. Behavior—physiology. 3. Psychophysiology.
LC Classification not assigned
612.8—dc23 2012036987
10 9 8 7 6 5 4 3 2 1

Student Versions:
Hard Cover: 978-0-205-94024-0
0-205-94024-2
Paper Cover: 978-0-205-94799-7
0-205-94799-9
Books a la Carte: 978-0-205-94040-0
0-205-94040-4

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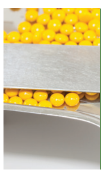

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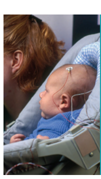

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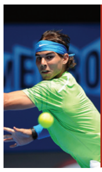

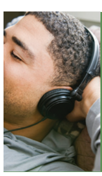

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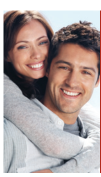

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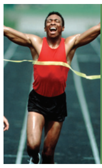

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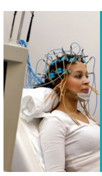

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PREFACE

All my life I have wanted to know how things work. When I was a boy I took apart alarm clocks, radios, my mother's sewing machine, and other interesting gadgets to see what was inside. Much to my parents' relief, I outgrew that habit (or at least got better at putting things back together), but my curiosity is still with me. Since my college days, I have been trying to find out all I can about the workings of the most intricate piece of machinery that we know of: the human brain.

The field of neuroscience research is a very busy and productive one today. A large number of scientists are trying to understand the physiology of behavior, using more and more advanced methods, yielding more and more interesting results. Their findings provide me with much to write about. I admire their dedication and hard work, and I thank them for giving me something to say. Without their efforts I could not have written this book.

I wrote the first edition of this book at the request of my colleagues who teach the course and wanted a briefer version of *Physiology of Behavior* with more emphasis on research related to humans. The first part of this book is concerned with foundations: the history of the field, the structure and functions of neurons, neuroanatomy, psychopharmacology, and methods of research. The second part is concerned with inputs: the sensory systems. The third part deals with what might be called "motivated" behavior: sleep, reproduction, emotion, and ingestion. The fourth part deals with learning and verbal communication. The final part deals with neurological and mental disorders.

New to This Edition

Of course, all chapters in this book have been revised. My colleagues keep me busy by providing me with interesting research results to describe in my book. The challenge is always to include the interesting new material without letting the length of the book get out of hand.

The following list includes some of the information that is new to this edition:

- Role of prion proteins in normal brain development
- Research on optogenetic methods to restore sight in blinded animals
- Congenital amusia
- Increased auditory input to the visual cortex in blind people
- Musical processing in the brains of newborn infants
- Neural mechanisms of homeostatic, allostatic, and circadian factors in control of sleep
- Role of kisspeptin in onset of puberty
- Role of the ventromedial prefrontal cortex in extinction of conditioned emotional responses
- Role of 5-HT in moral judgments
- Cross-cultural recognition of nonverbal emotional vocalizations
- Identification of osmoreceptors involved in thirst
- Research on genes involved in regulation of body weight
- Role of PKM-zeta in long-term potentiation and learning
- Role of place cells, grid cells, head-direction cells, and border cells in spatial learning
- Research on brain mechanisms of recognition of people's voices
- Research on universal features of written languages
- New section on traumatic brain injury
- Mirror neurons and therapy after stroke
- Research on use of small interfering RNA for treatment of Huntington's disease
- Role of prion-like transmission of misfolded Aβ in Alzheimer's disease
- Trial of gene delivery to the basal ganglia to treat Parkinson's disease

- Role of glial infection in AIDS dementia complex
- Role of DISC1 mutation in schizophrenia and depression
- Effect of season of birth on development of depression
- Effects of oxytocin on social interaction in autistic disorders
- Role of COMT gene in susceptibility to PTSD
- Treatment of PTSD with TMS
- Role of MCH and orexin in the appetite-reducing effects of nicotine
- Role of alleles of the α5 ACh gene in nicotine addiction
- Research on the use of DBS and TMS in treatment of drug addiction

Strategies for Learning

This theme of strategies for learning, which runs throughout the book, was created to help apply the research findings of behavioral neuroscience to daily life. For example, in Chapter 1 you will find a section called *Strategies for Learning*; and in Chapter 5, *Methods and Strategies of Research*, you will find that you are not faced with a bewildering list of research methods; instead, you are led through a set of hypothetical investigations organized the way that a research project might proceed. Each step in an investigation illustrates a particular procedure in the context in which it would be applied in an ongoing program.

The following sections in each chapter provide an overview of the chapter as well as a convenient review of the subjects covered.

- **LEARNING OBJECTIVES.** Each chapter begins with a list of Learning Objectives that also serve as the framework for the study guide that accompanies this text.
- **PROLOGUE.** Each chapter opens with a Prologue that contains the description of an episode involving a neurological disorder or an issue in neuroscience.
- **EPILOGUE.** At the end of the chapter, an Epilogue resolves the issues raised in the Prologue, discussing them in terms of what the reader has learned in the chapter, or it introduces a related topic.
- **SECTION SUMMARY.** A Section Summary follows each major section of the book. The summaries not only provide useful reviews, but they also break each chapter into manageable chunks.
- **THOUGHT QUESTIONS.** Most Interim Summaries are followed by Thought Questions. The questions provide students with an opportunity to think about what they have learned in the previous section.
- **KEY TERMS.** Definitions of Key Terms are printed in the margin on the page in the text where the terms are first discussed or on a facing page. For terms that might be difficult to pronounce, a pronunciation guide is included with the definition.
- **KEY CONCEPTS.** Each chapter ends with a Key Concepts section that provides a quick review of the topics discussed in the chapter.

Pedagogically Sound Art

Jay Alexander, of I-Hua Graphics, prepared the illustrations in this book. Jay and I have been working together on my books for several years. I think the result of our collaboration is a set of clear, attractive, and pedagogically effective illustrations.

Resources for Instructors

Several supplements are available for instructors who adopt this book.

- **INSTRUCTOR'S MANUAL** (ISBN 0-205-94035-8) Written by Scott Wersinger, State University of New York at Buffalo, this manual provides a tool for classroom preparation and management. Each chapter includes an Integrated Teaching Outline with teaching objectives, lecture material, demonstrations and activities, handouts, videos, suggested readings, web resources, and information about other supplements. Available online at www.pearsonhighered.com/irc.
- **TEST BANK** (ISBN 0-205-94036-6) Written by Paul Wellman, Texas A&M University, this resource contains questions that target key concepts. Each chapter has approximately 100 questions, including multiple choice, true/false, short answer, and essay—each with an answer justification, page references, difficulty rating, and type designation. All questions are correlated to both chapter learning objectives and APA learning objectives. The Test Bank is also available in Pearson MyTest (ISBN 0205940374), a powerful online assessment software program. Instructors can easily create and print quizzes and exams as well as author new questions online for maximum flexibility. Both the Test Bank and MyTest are available online at www.pearsonhighered.com/irc.
- **POWERPOINT SLIDES** (ISBN 0-205-94034-X) Created by Grant McLaren, Edinboro University of Pennsylvania, this interactive tool facilitates the development of lectures and the encouragement of classroom discussions by pairing key points covered in the chapters with images from the text. For this edition, the slides have been enhanced with even more visual appeal to engage students. Available online at www.pearsonhighered.com/irc.

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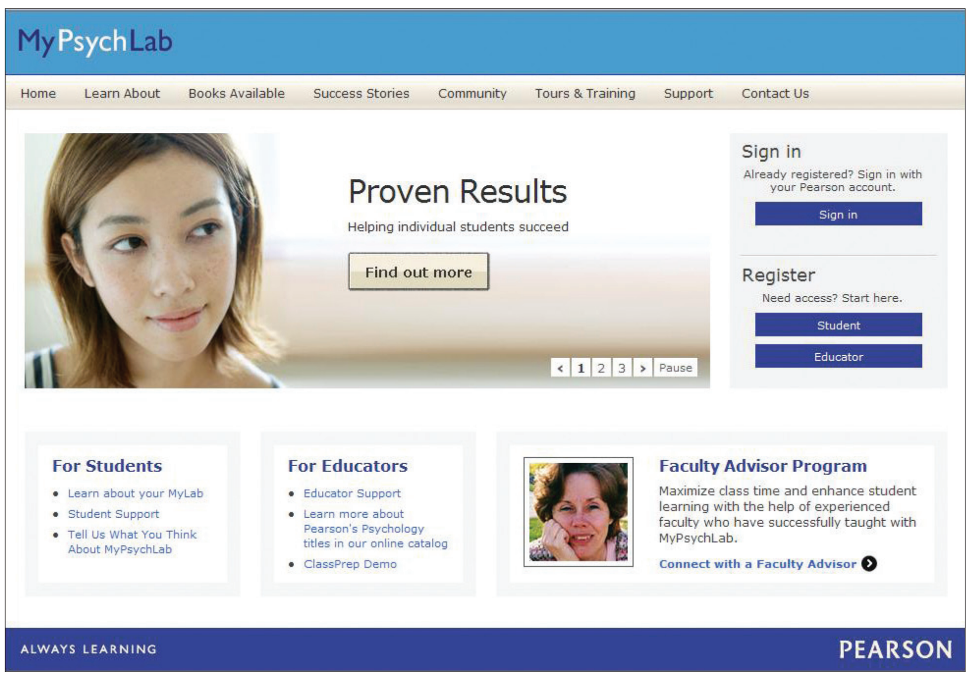

MyPsychLab (www.mypsychlab.com)

MyPsychLab is an online homework, tutorial, and assessment program that truly engages students in learning. It helps students better prepare for class, quizzes, and exams—resulting in better performance in the course. It provides educators with a dynamic set of tools for gauging individual and class performance.

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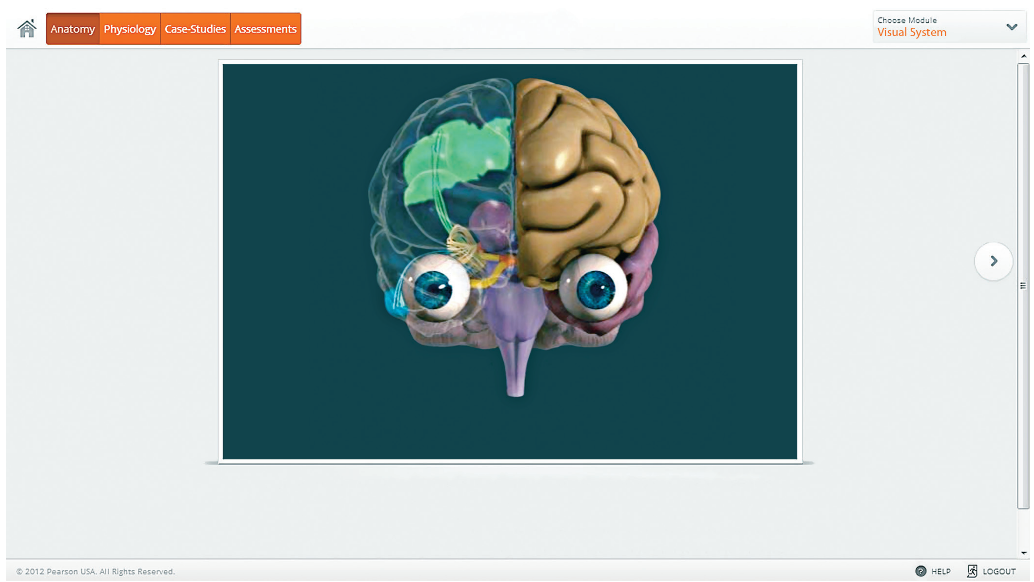
- **BLACKBOARD SINGLE SIGN-ON.** MyPsychLab can be used by itself or linked to any course management system. Blackboard single sign-on provides deep linking to all New MyPsychLab resources.
- **PEARSON ETEXT AND CHAPTER AUDIO.** Like the printed text, students can highlight relevant passages and add notes. The Pearson eText can be accessed through laptops, iPads,

and tablets. Download the free Pearson eText app to use on tablets. Students can also listen to their text with the Audio eText.

- **ASSIGNMENT CALENDAR & GRADEBOOK.** A drag-and-drop assignment calendar makes assigning and completing work easy. The automatically graded assessment provides instant feedback and flows into the gradebook, which can be used in the MyPsychLab or exported.
- **PERSONALIZED STUDY PLAN.** Students' personalized plans promote better critical thinking skills. The study plan organizes students' study needs into sections, such as Remembering, Understanding, Applying, and Analyzing.
- **MYPSYCHLAB MARGIN ICONS.** Margin icons guide students from their reading material to relevant videos and simulations.

The new ***MyPsychLab Brain*** is an interactive virtual brain designed to help students better understand neuroanatomy, physiology, and human behavior. Fifteen new modules bring to life many of the most difficult topics typically covered in the biopsychology course. Every module includes sections that explore relevant anatomy, physiological animations, and engaging case studies that bring behavioral neuroscience to life. At the end of each module, students can take an assessment that will help them measure their understanding. This hands-on experience engages students and helps make course content and terminology relevant. References throughout the text direct students to content in MyPsychLab, and a new feature at the end of each chapter directs students to ***MyPsychLab Brain*** modules.



In Conclusion

Trying to keep up with the rapid progress being made in neuroscience research poses a challenge for teachers and textbook writers. If a student simply memorizes what we believe at the time to be facts, he or she is left with knowledge that quickly becomes obsolete. In this book I have tried to provide enough background material and enough knowledge of basic physiological processes that the reader can revise what he or she has learned when research provides us with new information.

I designed this text to be interesting and informative. I have endeavored to provide a solid foundation for further study. Students who will not take subsequent courses in this or related fields should receive the satisfaction of a much better understanding of their own behavior. Also, they will have a greater appreciation for the forthcoming advances in medical practices related to disorders that affect a person's perception, mood, or behavior. I hope that people who read this book carefully will henceforth perceive human behavior in a new light.

Acknowledgments

Although I must accept the blame for any shortcomings of the book, I want to thank colleagues who helped me with this book by sending reprints of their work, suggesting topics that I should cover, sending photographs that have been reproduced in this book, and pointing out deficiencies in the previous edition. I thank the following reviewers for their comments on this edition:

John Agnew, University of Colorado at Boulder
Robert Berks, Granite State College
Melissa Birkett, Northern Arizona University
Ann Cohen, University of Pittsburgh
Bradley Cooke, Georgia State University
Kristen D'Anci, Salem State University
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I also want to thank the people at Pearson: Amber Chow, acquisitions editor; Nicole Kunzmann, marketing manager; Diane Szulecki, editorial project manager; Sherry Lewis and Roxanne Klaas, production project managers; and Chris Feldman, copy editor. I must also thank my wife Mary for her support. Writing is a lonely pursuit, because one must be alone with one's thoughts for many hours of the day. I thank her for giving me the time to read, reflect, and write without feeling that I was neglecting her too much.

To the Reader

I hope that in reading this book you will come not only to learn more about the brain but also to appreciate it for the marvelous organ it is. The brain is wonderfully complex, and perhaps the most remarkable thing is that we are able to use it in our attempt to understand it.

While working on this book, I imagined myself talking with students, telling them interesting stories about the findings of clinicians and research scientists. Imagining your presence made the task of writing a little less lonely. I hope that the dialogue will continue. Please write to me and tell me what you like and dislike about the book. My e-mail address is nrc@psych.umass.edu. If you write to me, we can make the conversation a two-way exchange.

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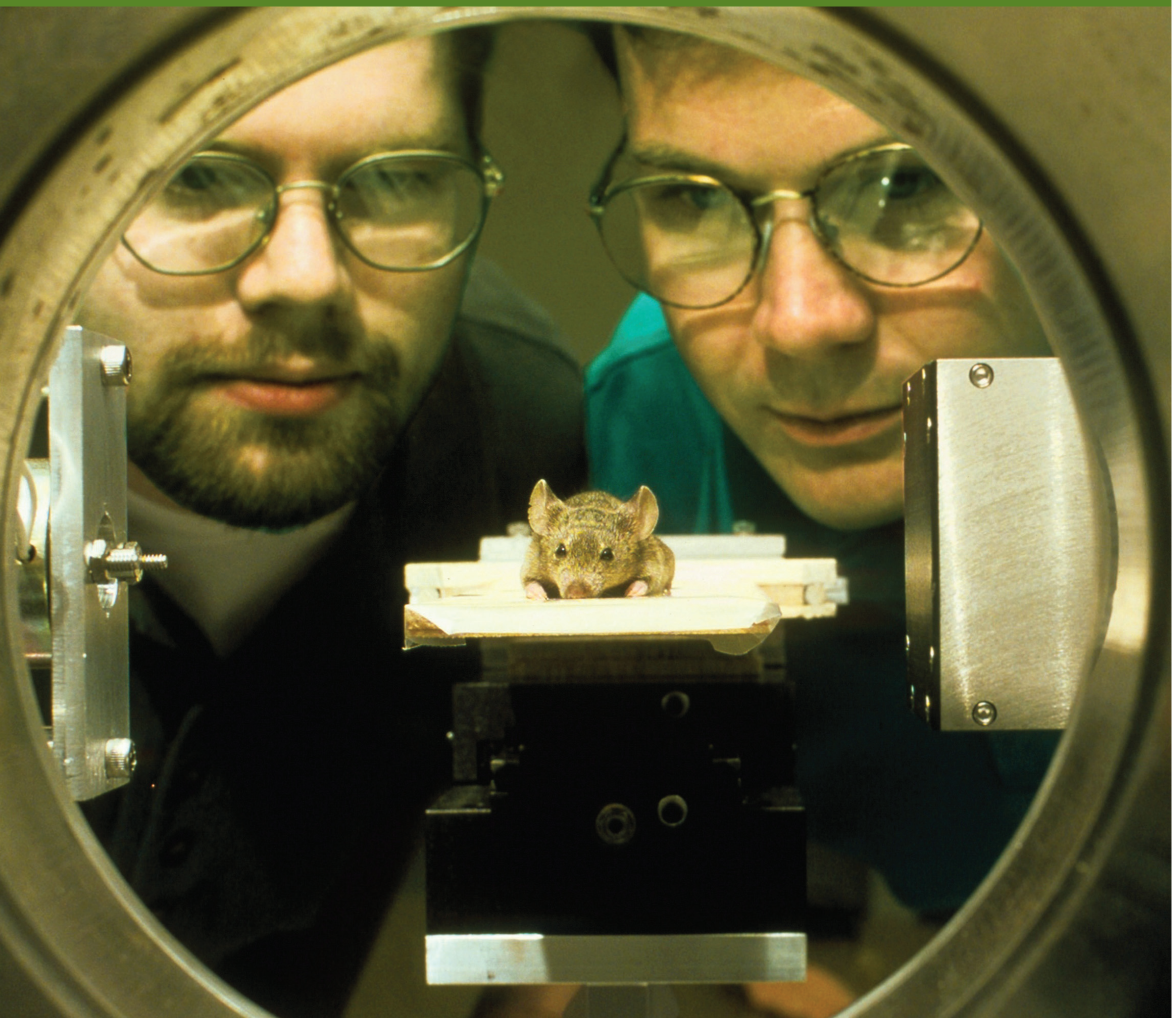
CHAPTER

1 Origins of Behavioral Neuroscience



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OUTLINE

LEARNING OBJECTIVES

1. Describe the behavior of people with split brains and explain what study of this phenomenon contributes to our understanding of self-awareness.
2. Describe the goals of scientific research.
3. Describe the biological roots of behavioral neuroscience.
4. Describe the role of natural selection in the evolution of behavioral traits.
5. Describe the evolution of the human species.
6. Discuss the value of research with animals and ethical issues concerning their care.
7. Describe career opportunities in neuroscience.
8. Outline the strategies that will help you learn as much as possible from this book.

PROLOGUE | René's Inspiration

René, a lonely and intelligent young man of eighteen years, had secluded himself in Saint-Germain, a village to the west of Paris. He had recently suffered a nervous breakdown and chose the retreat to recover. Even before coming to Saint-Germain, he had heard of the fabulous royal gardens built for Henri IV and Marie de Médicis, and one sunny day he decided to visit them. The guard stopped him at the gate, but when he identified himself as a student at the King's School at La Flèche, he was permitted to enter. The gardens consisted of a series of six large terraces overlooking the Seine, planted in the symmetrical, orderly fashion so loved by the French. Grottoes were cut into the limestone hillside at the end of each terrace; René entered one of them. He heard eerie music accompanied by the gurgling of water but at first could see nothing in the darkness. As his eyes became accustomed to the gloom, he could make out a figure illuminated by a flickering torch. He approached the figure, which he soon recognized as that of a young woman. As he drew closer, he saw that she was actually a bronze statue of Diana, bathing in a pool of water. Suddenly, the Greek goddess fled and hid behind a bronze rosebush. As René pursued her, an imposing statue of Neptune rose in front of him, barring the way with his trident.

René was delighted. He had heard about the hydraulically operated mechanical organs and the moving statues, but he had not expected such realism. As he walked back toward the entrance to the grotto, he saw the plates buried in the ground that controlled the valves operating the machinery. He spent the rest of the afternoon wandering through the grottoes, listening to the music and being entertained by the statues.

During his stay in Saint-Germain, René visited the royal gardens again and again. He had been thinking about the relationship between the movements of animate and inanimate objects, which had concerned philosophers for some time. He thought he saw in the apparently purposeful, but obviously inanimate, movements of the statues an answer to some important questions about the relationship between the mind and the body. Even after he left Saint-Germain, René Descartes revisited the grottoes in his memory. He even went so far as to name his daughter Francine after their designers, the Francini brothers of Florence.

The last frontier in this world—and perhaps the greatest one—lies within us. The human nervous system makes possible all that we can do, all that we can know, and all that we can experience. Its complexity is immense, and the task of studying it and understanding it dwarfs all previous explorations our species has undertaken.

One of the most universal of all human characteristics is curiosity. We want to explain what makes things happen. In ancient times, people believed that natural phenomena were caused by animating spirits. All moving objects—animals, the wind and tides, the sun, moon, and stars—were assumed to have spirits that caused them to move. For example, stones fell when they were dropped because their animating spirits wanted to be reunited with Mother Earth. As our ancestors became more sophisticated and learned more about nature, they abandoned this approach (which we call *animism*) in favor of physical explanations for inanimate moving objects. But they still used spirits to explain human behavior.

From the earliest historical times, people have believed that they possessed something intangible that animated them—a mind, a soul, or a spirit. This belief stems from the fact that each of us is aware of our own existence. When we think or act, we feel as though something inside us is thinking or deciding to act. But what is the nature of the human mind? We have physical bodies with muscles that move them and sensory organs such as eyes and ears that perceive information about the world around us. Within our bodies the nervous system plays a central role, receiving information from the sensory organs and controlling the movements of the muscles. But what is the mind, and what role does it play? Does it *control* the nervous system? Is it a *part of* the nervous system? Is it physical and tangible, like the rest of the body, or is it a spirit that will always remain hidden?

Behavioral neuroscientists take an empirical and practical approach to the study of human nature. Most of us believe that the mind is a phenomenon produced by the workings of the nervous system. We believe that once we understand the workings of the human body—especially the workings of the nervous system—we will be able to explain how we perceive, how we think, how we remember, and how we act. We will even be able to explain the nature of our own self-awareness. Of course, we are far from understanding the workings of the nervous system, so only time will tell whether this belief is justified.

Scientists and engineers have developed research methods that enable neuroscientists to study activity of the human brain.

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Understanding Human Consciousness: A Physiological Approach

How can behavioral neuroscientists study human consciousness? First, let's define our terms. The word *consciousness* can be used to refer to a variety of concepts, including simple wakefulness. Thus, a researcher may write about an experiment using "conscious rats," referring to the fact that the rats were awake and not anesthetized. By *consciousness,* I am referring to something else: the fact that we humans are aware of—and can tell others about—our thoughts, perceptions, memories, and feelings.

We know that brain damage or drugs can profoundly affect consciousness. Because consciousness can be altered by changes in the structure or chemistry of the brain, we may hypothesize that consciousness is a physiological function, just as behavior is. We can even speculate about the origins of this self-awareness. Consciousness and the ability to communicate seem to go hand in hand. Our species, with its complex social structure and enormous capacity for learning, is well served by our ability to communicate: to express intentions to one another and to make requests of one another. Verbal communication makes cooperation possible and permits us to establish customs and laws of behavior. Perhaps the evolution of this ability is what has given rise to the phenomenon of consciousness. That is, our ability to send and receive messages with other people enables us to send and receive our own messages inside our own heads—in other words, to think and to be aware of our own existence. (See ***Figure 1.1***.)

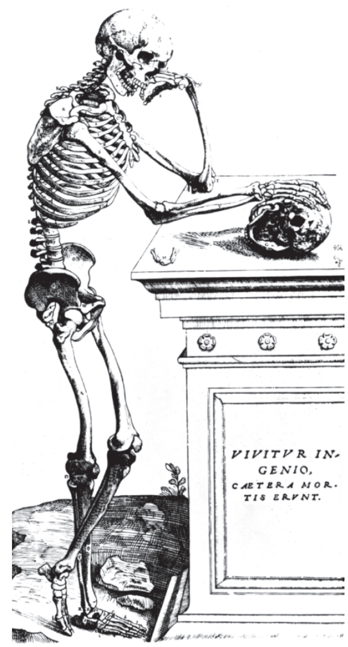

FIGURE 1.1 Studying the Brain. Will the human brain ever completely understand its own workings? A sixteenth-century woodcut from the first edition of *De humani corporis fabrica (On the Workings of the Human Body)* by Andreas Vesalius.

National Library of Medicine.

Split Brains

Studies of humans who have undergone a particular surgical procedure demonstrate dramatically how disconnecting parts of the brain that are involved with perceptions from parts involved with verbal behavior also disconnects them from consciousness. These results suggest that the parts of the brain involved in verbal behavior may be the ones responsible for consciousness.

The surgical procedure is one that has been used for people with very severe epilepsy that cannot be controlled by drugs. In these people, nerve cells in one side of the brain become overactive, and the overactivity is transmitted to the other side of the brain by a structure called the corpus callosum. The **corpus callosum** is a large bundle of nerve fibers that connects corresponding parts of one side of the brain with those of the other. Both sides of the brain then engage in wild activity and stimulate each other, causing a generalized epileptic seizure. These seizures can occur many times each day, preventing the person from leading a normal life. Neurosurgeons discovered that cutting the corpus callosum (the **split-brain operation**) greatly reduced the frequency of the epileptic seizures.

corpus callosum (***core*** *pus ka* ***low*** *sum*) A large bundle of nerve fibers that connects corresponding parts of one side of the brain with those of the other.

split-brain operation Brain surgery that is occasionally performed to treat a form of epilepsy; the surgeon cuts the corpus callosum, which connects the two hemispheres of the brain.

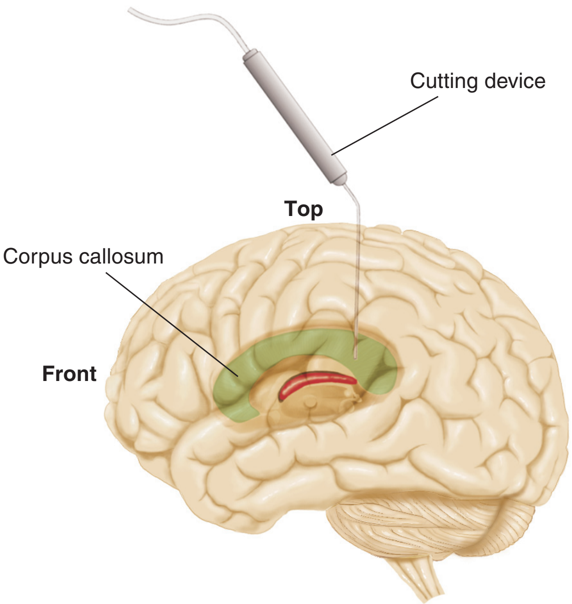

FIGURE 1.2 **The Split-Brain Operation.** A "window" has been opened in the side of the brain so that we can see the corpus callosum being cut at the midline of the brain.

Figure 1.2 shows a drawing of the split-brain operation. We see the brain being sliced down the middle, from front to back, dividing it into its two symmetrical halves. A "window" has been opened in the left side of the brain so that we can see the corpus callosum being cut by the neurosurgeon's special knife. (See ***Figure 1.2***.)

Sperry (1966) and Gazzaniga and his associates (Gazzaniga and LeDoux, 1978; Gazzaniga, 2005) have studied these patients extensively. The largest part of the brain consists of two symmetrical parts, called the **cerebral hemispheres**, which receive sensory information from the opposite sides of the body. They also control movements of the opposite sides. The corpus callosum enables the two hemispheres to share information so that each side knows what the other side is perceiving and doing. After the split-brain operation is performed, the two hemispheres are disconnected and operate independently. Their sensory mechanisms, memories, and motor systems can no longer exchange information. The effects of these disconnections are not obvious to the casual observer, for the simple reason that only one hemisphere—in most people, the left—controls speech. The right hemisphere of an epileptic person with a split brain appears to be able to understand verbal instructions reasonably well, but it is incapable of producing speech.

Because only one side of the brain can talk about what it is experiencing, people who speak with a person with a split brain are conversing with only one hemisphere: the left. The actions of the right hemisphere are more difficult to detect. Even the patient's left hemisphere has to learn about the independent existence of the right hemisphere. One of the first things that these patients say they notice after the operation is that their left hand seems to have a "mind of its own." For example, patients may find themselves putting down a book held in the left hand, even if they have been reading it with great interest. This conflict occurs because the right hemisphere, which controls the left hand, cannot read and therefore finds the book boring. At other times, these patients surprise themselves by making obscene gestures (with the left hand) when they do not intend to. A psychologist once reported that a man with a split brain had attempted to beat his wife with one hand and protect her with the other. Did he *really* want to hurt her? Yes and no, I guess.

cerebral hemispheres The two symmetrical halves of the brain; they constitute the major part of the brain.

One exception to the crossed representation of sensory information is the olfactory system. That is, when a person sniffs a flower through the left nostril, only the left brain receives a sensation of the odor. Thus, if the right nostril of a patient with a split brain is closed, leaving only the left nostril open, the patient will be able to tell us what the odors are (Gordon and Sperry, 1969). However, if the odor enters the right nostril, the patient will say that he or she smells nothing. But, in fact, the right brain *has* perceived the odor and *can* identify it. To show this, we ask the patient to smell an odor with the right nostril and then reach for some objects that are hidden from view by a partition. If asked to use the left hand, controlled by the hemisphere that detected the smell, the patient will select the object that corresponds to the odor—a plastic flower for a floral odor, a toy fish for a fishy odor, a model tree for the odor of pine, and so forth. But if asked to use the right hand, the patient fails the test because the right hand is connected to the left hemisphere, which did not smell the odor. (See ***Figure 1.3***.)

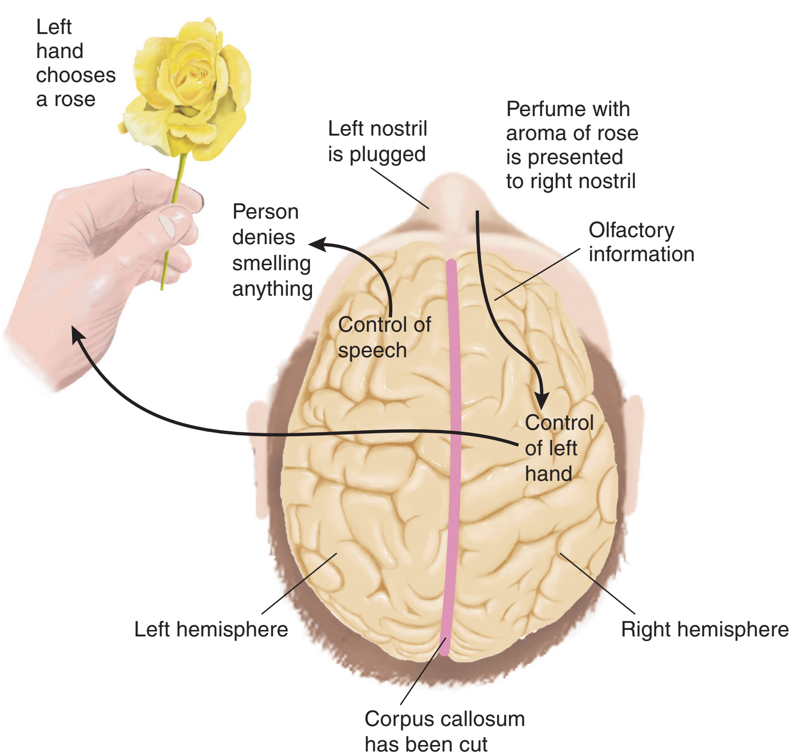

FIGURE 1.3 **Smelling with a Split Brain.** Identification of an object occurs in response to an olfactory stimulus by a person with a split brain.

The effects of cutting the corpus callosum reinforce the conclusion that we become conscious of something only if information about it is able to reach the parts of the brain responsible for verbal communication, which are located in the left hemisphere. If the information does not reach these parts of the brain, then that information does not reach the consciousness associated with these mechanisms. We still know very little about the physiology of consciousness, but studies of people with brain damage are beginning to provide us with some useful insights. This issue is discussed in later chapters.

SECTION SUMMARY

Understanding Human Consciousness: A Physiological Approach

The concept of the mind has been with us for a long time—probably from the earliest history of our species. Modern science has concluded that the world consists of matter and energy and that what we call the mind can be explained by the same laws that govern all other natural phenomena. Studies of the functions of the human nervous system tend to support this position, as the specific example of the split brain shows. Brain damage, by disconnecting brain functions from the speech mechanisms in the left hemisphere, reveals that the mind does not have direct access to all brain functions.

When sensory information about a particular object is presented only to the right hemisphere of a person who has had a split-brain operation, the person is not aware of the object but can, nevertheless, indicate by movements of the left hand that the object has been perceived. This phenomenon suggests that consciousness involves operations of the verbal mechanisms of the left hemisphere. Indeed, consciousness may be, in large part, a matter of us "talking to ourselves." Thus, once we understand the language functions of the brain, we may have gone a long way to understanding how the brain can be conscious of its own existence.

Thought Questions

1. Could a sufficiently large and complex computer ever be programmed to be aware of itself? Suppose that someone someday claims to have done just that. What kind of evidence would you need to prove or disprove this claim?
2. Is consciousness found in animals other than humans? Is the ability of some animals to communicate with each other and with humans evidence for at least some form of awareness of self and others?
3. Clearly, the left hemisphere of a person with a split brain is conscious of the information it receives and of its own thoughts. It is not conscious of the mental processes of the right hemisphere. But is it possible that the right hemisphere is conscious too, but is just unable to talk to us? How could we possibly find out whether it is? Do you see some similarities between this issue and the one raised in the first question?

The Nature of Behavioral Neuroscience

The modern history of behavioral neuroscience has been written by psychologists who have combined the experimental methods of psychology with those of physiology and have applied them to the issues that concern all psychologists. Thus, we have studied perceptual processes, control of movement, sleep and waking, reproductive behaviors, ingestive behaviors, emotional behaviors, learning, and language. In recent years we have also begun to study the physiology of pathological conditions, such as addictions and mental disorders.

The Goals of Research

The goal of all scientists is to explain the phenomena they study. But what do we mean by *explain*? Scientific explanation takes two forms: generalization and reduction. Most psychologists deal with **generalization**. They explain particular instances of behavior as examples of general laws, which they deduce from their experiments. For instance, most psychologists would explain a pathologically strong fear of dogs as an example of a particular form of learning called *classical conditioning*. Presumably, the person was frightened earlier in life by a dog. An unpleasant stimulus was paired with the sight of the animal (perhaps the person was knocked down by an exuberant dog or was attacked by a vicious one), and the subsequent sight of dogs evokes the earlier response: fear.

Most physiologists deal with **reduction**. They explain complex phenomena in terms of simpler ones. For example, they may explain the movement of a muscle in terms of the changes in the membranes of muscle cells, the entry of particular chemicals, and the interactions among protein molecules within these cells. By contrast, a molecular biologist would explain these events in terms of forces that bind various molecules together and cause various parts of the molecules to be attracted to one another. In turn, the job of an atomic physicist is to describe matter and

generalization Type of scientific explanation; a general conclusion based on many observations of similar phenomena.

reduction Type of scientific explanation; a phenomenon is described in terms of the more elementary processes that underlie it.

Studies of people with brain damage have given us insights into the brain mechanisms involved in language, perception, memory, and emotion.

Neil Carlson.

energy themselves and to account for the various forces found in nature. Practitioners of each branch of science use reduction to call on sets of more elementary generalizations to explain the phenomena they study.

The task of the behavioral neuroscientist is to explain behavior in physiological terms. But behavioral neuroscientists cannot simply be reductionists. It is not enough to observe behaviors and correlate them with physiological events that occur at the same time. Identical behaviors may occur for different reasons and thus may be initiated by different physiological mechanisms. Therefore, we must understand "psychologically" why a particular behavior occurs before we can understand what physiological events made it occur.

Let me provide a specific example: Mice, like many other mammals, often build nests. Behavioral observations show that mice will build nests under two conditions: when the air temperature is low and when the animal is pregnant. A nonpregnant mouse will build a nest only if the weather is cool, whereas a pregnant mouse will build one regardless of the temperature. The same behavior occurs for different reasons. In fact, nest-building behavior is controlled by two different physiological mechanisms. Nest building can be studied as a behavior related to the process of temperature regulation, or it can be studied in the context of parental behavior.

In practice, the research efforts of behavioral neuroscientists involve both forms of explanation: generalization and reduction. Ideas for experiments are stimulated by the investigator's knowledge both of psychological generalizations about behavior and of physiological mechanisms. A good behavioral neuroscientist must therefore be both a good psychologist *and* a good physiologist.

Biological Roots of Behavioral Neuroscience

Study of (or speculations about) the physiology of behavior has its roots in antiquity. Because its movement is necessary for life, and because emotions cause it to beat more strongly, many ancient cultures, including the Egyptian, Indian, and Chinese, considered the heart to be the seat of thought and emotions. The ancient Greeks did, too, but Hippocrates (460–370 B.C.) concluded that this role should be assigned to the brain.

Not all ancient Greek scholars agreed with Hippocrates. Aristotle did not; he thought the brain served to cool the passions of the heart. But Galen (A.D. 130–200), who had the greatest respect for Aristotle, concluded that Aristotle's role for the brain was "utterly absurd, since in that case Nature would not have placed the encephalon [brain] so far from the heart, . . . and she would not have attached the sources of all the senses [the sensory nerves] to it" (Galen, 1968 translation, p. 387). Galen thought enough of the brain to dissect and study the brains of cattle, sheep, pigs, cats, dogs, weasels, monkeys, and apes (Finger, 1994).

René Descartes, a seventeenth-century French philosopher and mathematician, has been called the father of modern philosophy. Although he was not a biologist, his speculations about the roles of the mind and brain in the control of behavior provide a good starting point in the history of behavioral neuroscience. Descartes assumed that the world was a purely mechanical entity that, once having been set in motion by God, ran its course without divine interference. Thus, to understand the world, one had only to understand how it was constructed. To Descartes, animals were mechanical devices; their behavior was controlled by environmental stimuli. His view of the human body was much the same: It was a machine. As Descartes observed, some movements of the human body were automatic and involuntary. For example, if a person's finger touched a hot object, the arm would immediately withdraw from the source of stimulation. Reactions like this did not require participation of the mind; they occurred automatically. Descartes called these actions **reflexes** (from the Latin *reflectere,* "to bend back upon itself"). Energy coming from the outside source would be reflected back through the nervous system to the muscles, which would contract. The term is still in use today, but of course we explain the operation of a reflex differently.

reflex An automatic, stereotyped movement produced as the direct result of a stimulus.

Like most philosophers of his time, Descartes believed that each person possesses a mind—a uniquely human attribute that is not subject to the laws of the universe. But his thinking differed from that of his predecessors in one important way: He was the first to suggest that a link exists between the human mind and its purely physical housing, the brain. He believed that the sense organs of the body supply the mind with information about what is happening in the environment, and that the mind, using this information, controls the body's movements. In particular, he hypothesized that the interaction between mind and body takes place in the pineal body, a small organ situated on top of the brain stem, buried beneath the cerebral hemispheres. He noted that the brain contains hollow chambers (the *ventricles*) that are filled with fluid, and he believed that this fluid was under pressure. In his theory, when the mind decides to perform an action, it tilts the pineal body in a particular direction like a little joystick, causing pressurized fluid to flow from the brain into the appropriate set of nerves. This flow of fluid causes the same muscles to inflate and move. (See ***Figure 1.4***.)

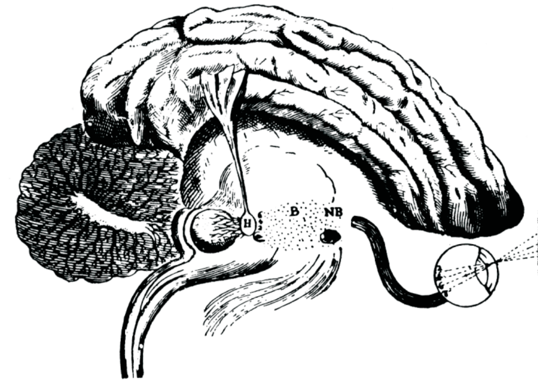

FIGURE 1.4 Descartes's Theory. This woodcut appears in *De homine* by René Descartes, which was published in 1662. Descartes believed that the "soul" (what we would today call the *mind*) controls the movements of the muscles through its influence on the pineal body. According to his theory, the eyes sent visual information to the brain, where it could be examined by the soul. When the soul decided to act, it would tilt the pineal body (labeled H in the diagram), which would divert pressurized fluid through nerves to the appropriate muscles. His explanation is modeled on the mechanism that animated statues in the royal gardens near Paris.

As we saw in the prologue, the young René Descartes was greatly impressed by the moving statues in the royal gardens (Jaynes, 1970). These devices served as models for Descartes in theorizing about how the body worked. The pressurized water of the moving statues was replaced by pressurized fluid in the ventricles; the pipes were replaced by nerves; the cylinders by muscles; and finally, the hidden valves by the pineal body. This story illustrates one of the first times that a technological device was used as a model for explaining how the nervous system works. In science, a **model** is a relatively simple system that works on known principles and is able to do at least some of the things that a more complex system can do. For example, when scientists discovered that elements of the nervous system communicate by means of electrical impulses, researchers developed models of the brain based upon telephone switchboards and, more recently, computers. Abstract models, which are completely mathematical in their properties, have also been developed.

Descartes's model was useful because, unlike purely philosophical speculations, it could be tested experimentally. In fact, it did not take long for biologists to prove that Descartes was wrong. Luigi Galvani, a seventeenth-century Italian physiologist, found that electrical stimulation of a frog's nerve caused contraction of the muscle to which it was attached. Contraction occurred even when the nerve and muscle were detached from the rest of the body; therefore, Galvani concluded that the muscle's ability to contract and the nerve's ability to send a message to the muscle were characteristics of these tissues themselves. Thus, the brain did not inflate muscles by directing pressurized fluid through the nerve. Galvani's experiment prompted others to study the nature of the message transmitted by the nerve and the means by which muscles contracted. The results of these efforts gave rise to an accumulation of knowledge about the physiology of behavior.

FIGURE 1.5 Johannes Müller (1801–1858).

One of the most important figures in the development of experimental physiology was Johannes Müller, a nineteenth-century German physiologist. (See ***Figure 1.5***.) Müller was a forceful advocate of the application of experimental techniques to physiology. Previously, the activities of most natural scientists were limited to observation and classification. Although these activities are essential, Müller insisted that major advances in our understanding of the workings of the body would be achieved only by experimentally removing or isolating animals' organs, testing their responses to various chemicals, and otherwise altering the environment to see how the organs responded. His most important contribution to the study of the physiology of behavior was his **doctrine of specific nerve energies**. Müller observed that although all nerves carry the same basic message—an electrical impulse—we perceive the messages of different nerves in different ways. For example, messages carried by the optic nerves produce sensations of visual images, and those carried by the auditory nerves produce sensations of sounds. How can different sensations arise from the same basic message?

The answer is that the messages occur in different channels. The portion of the brain that receives messages from the optic nerves interprets the activity as visual stimulation, even if the nerves are actually stimulated mechanically. (For example, when we rub our eyes, we see flashes of light.) Because different parts of the brain receive messages from different nerves, the brain must be functionally divided: Some parts perform some functions, while other parts perform others.

Müller's advocacy of experimentation and the logical deductions from his doctrine of specific nerve energies set the stage for performing experiments directly on the brain. Indeed, Pierre Flourens,

model A mathematical or physical analogy for a physiological process; for example, computers have been used as models for various functions of the brain.

doctrine of specific nerve energies Müller's conclusion that because all nerve fibers carry the same type of message, sensory information must be specified by the particular nerve fibers that are active.

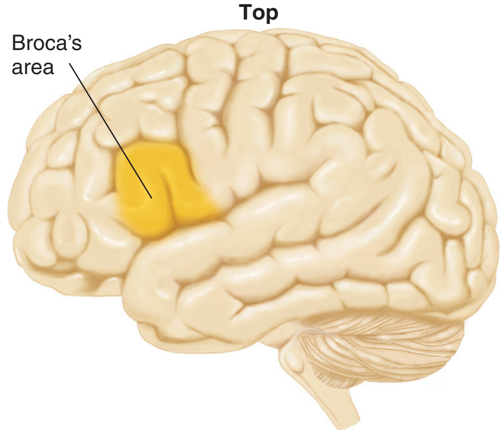

FIGURE 1.6 Broca's Area. This region of the brain is named for French surgeon Paul Broca, who discovered that damage to a part of the left side of the brain disrupted a person's ability to speak.

a nineteenth-century French physiologist, did just that. Flourens removed various parts of animals' brains and observed their behavior. By seeing what the animal could no longer do, he could infer the function of the missing portion of the brain. This method is called **experimental ablation** (from the Latin *ablatus,* "carried away"). Flourens claimed to have discovered the regions of the brain that control heart rate and breathing, purposeful movements, and visual and auditory reflexes.

Soon after Flourens performed his experiments, Paul Broca, a French surgeon, applied the principle of experimental ablation to the human brain. Of course, he did not intentionally remove parts of human brains to see how they worked. Instead, he observed the behavior of people whose brains had been damaged by strokes. In 1861 he performed an autopsy on the brain of a man who had had a stroke that resulted in the loss of the ability to speak. Broca's observations led him to conclude that a portion of the cerebral cortex on the front part of the left side of the brain performs functions necessary for speech. (See ***Figure 1.6***.) Other physicians soon obtained evidence supporting his conclusions. As you will learn in Chapter 13, the control of speech is not localized in a particular region of the brain. Indeed, speech requires many different functions, which are organized throughout the brain. Nonetheless, the method of experimental ablation remains important to our understanding of the brains of both humans and laboratory animals.

As I mentioned earlier, Luigi Galvani used electricity to demonstrate that muscles contain the source of the energy that powers their contractions. In 1870, German physiologists Gustav Fritsch and Eduard Hitzig used electrical stimulation as a tool for understanding the physiology of the brain. They applied weak electrical current to the exposed surface of a dog's brain and observed the effects of the stimulation. They found that stimulation of different portions of a specific region of the brain caused contraction of specific muscles on the opposite side of the body. We now refer to this region as the *primary motor cortex*, and we know that nerve cells there communicate directly with those that cause muscular contractions. We also know that other regions of the brain communicate with the primary motor cortex and thus control behaviors. For example, the region that Broca found necessary for speech communicates with, and controls, the portion of the primary motor cortex that controls the muscles of the lips, tongue, and throat, which we use to speak.

One of the most brilliant contributors to nineteenth-century science was the German physicist and physiologist Hermann von Helmholtz. Helmholtz devised a mathematical formulation of the law of conservation of energy; invented the ophthalmoscope (used to examine the retina of the eye); devised an important and influential theory of color vision and color blindness; and studied audition, music, and many physiological processes. Helmholtz was also the first scientist to attempt to measure the speed of conduction through nerves. Scientists had previously believed that such conduction was identical to the conduction that occurs in wires, traveling at approximately the speed of light. But Helmholtz found that neural conduction was much slower—only about ninety feet per second. This measurement proved that neural conduction was more than a simple electrical message, as we will see in Chapter 2.

Twentieth-century developments in experimental physiology include many important inventions, such as sensitive amplifiers to detect weak electrical signals, neurochemical techniques to analyze chemical changes within and between cells, and histological techniques to see cells and their constituents. Because these developments belong to the modern era, they are discussed in detail in subsequent chapters.

experimental ablation The research method in which the function of a part of the brain is inferred by observing the behaviors an animal can no longer perform after that part is damaged.

SECTION SUMMARY

The Nature of Behavioral Neuroscience

All scientists hope to explain natural phenomena. In this context, the term *explanation* has two basic meanings: generalization and reduction. Generalization refers to the classification of phenomena according to their essential features so that general laws can be formulated. For example, observing that gravitational attraction is related to the mass of two bodies and to the distance between them helps to explain the movement of planets. Reduction refers to the description of phenomena in terms of more basic physical processes. For example, gravitation can be explained in terms of forces and subatomic particles.

Behavioral neuroscientists use both generalization and reduction to explain behavior. In large part, generalizations use the traditional

Section Summary (*continued*)

methods of psychology. Reduction explains behaviors in terms of physiological events within the body—primarily within the nervous system. Thus, behavioral neuroscience builds upon the tradition of both experimental psychology and experimental physiology.

The behavioral neuroscience of today is rooted in important developments of the past. When René Descartes proposed a model of the brain based on hydraulically activated statues, his model stimulated observations that produced important discoveries. The results of Galvani's experiments eventually led to an understanding of the nature of the message transmitted by nerves between the brain and the sensory organs and muscles. Müller's doctrine of specific nerve energies paved the way for study of the functions of specific parts of the brain through the methods of experimental ablation and electrical stimulation.

Thought Questions

1. What is the value of studying the history of behavioral neuroscience? Is it a waste of time?
2. Suppose we studied just the latest research and ignored explanations that we now know to be incorrect. Would we be spending our time more profitably, or might we miss something?

Natural Selection and Evolution

Following the tradition of Müller and von Helmholtz, other biologists continued to observe, classify, and think about what they saw, and some of them arrived at valuable conclusions. The most important of these scientists was Charles Darwin. (See ***Figure 1.7***.) Darwin formulated the principles of *natural selection* and *evolution*, which revolutionized biology.

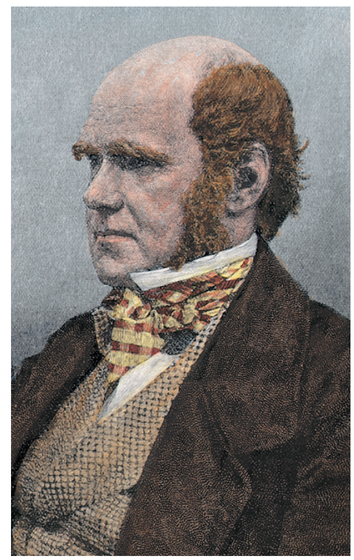

FIGURE 1.7 **Charles Darwin (1809–1882).** Darwin's theory of evolution revolutionized biology and strongly influenced early psychologists.

North Wind Picture Archives.

Functionalism and the Inheritance of Traits

Darwin's theory emphasized that all of an organism's characteristics—its structure, its coloration, its behavior—have functional significance. For example, the strong talons and sharp beaks of eagles permit them to catch and eat prey. Most caterpillars that eat green leaves are themselves green, and their color makes it difficult for birds to see them against their usual background. Mother mice construct nests, which keep their offspring warm and out of harm's way. Obviously, the behavior itself is not inherited—how can it be? What *is* inherited is a brain that causes the behavior to occur. Thus, Darwin's theory gave rise to **functionalism**, a belief that characteristics of living organisms perform useful functions. So, to understand the physiological basis of various behaviors, we must first discover what these behaviors accomplish. We must therefore understand something about the natural history of the species being studied so that the behaviors can be seen in context.

To understand the workings of a complex piece of machinery, we should know what its functions are. This principle is just as true for a living organism as it is for a mechanical device. However, an important difference exists between machines and organisms: Machines have inventors who had a purpose when they designed them, whereas organisms are the result of a long series of accidents. Thus, strictly speaking, we cannot say that any physiological mechanisms of living organisms have a *purpose*. But they do have *functions*, and these we can try to determine. For example, the forelimbs shown in Figure 1.8 are adapted for different uses in different species of mammals. (See ***Figure 1.8***.)

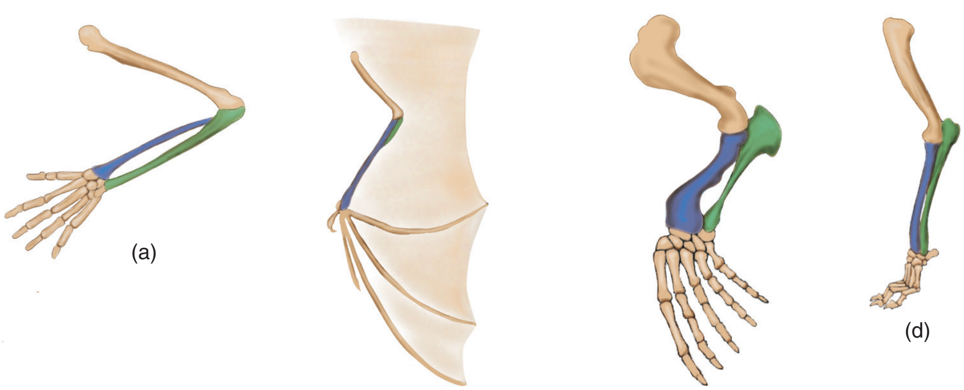

FIGURE 1.8 **Bones of the Forelimb.** The figure shows the bones of a (a) human, (b) bat, (c) whale, and (d) dog. Through the process of natural selection, these bones have been adapted to suit many different functions.

functionalism The principle that the best way to understand a biological phenomenon (a behavior or a physiological structure) is to try to understand its useful functions for the organism.